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Two types of genetic control over the development of shape

EDMUND W. SINNOTT AND SAMUEL KAISER

(WITH TWO TEXT FIGURES)

It is obvious that the specific shapes so characteristic of organic bodies and their various parts are as readily transmitted from parent to offspring by the processes of inheritance as are any other traits, but little is definitely known as to the mechanism by which this is accomplished. The problem is of particular biological interest since the persistence of these specific shapes is one of the most distinctive attributes of living organisms. Evidence is accumulating from various sources that shape inheritance is controlled by genes similar in character to those which have been postulated for other traits. One of the present authors (1922) has shown this to be true in the case of fruit shape in *Cucurbita*, and the other, on the basis of an extensive analysis, has found a similar situation in *Capsicum* fruits. Lindstrom (1927) has determined the position of a gene for fruit shape on one of the chromosomes of *Lycopersicum*. Other instances could be cited from studies of the inheritance of shape in leaves, flowers, fruits, roots, and other plant organs.

Although shape characters thus seem to present nothing unique in their inheritance, they are necessarily related more intimately to the processes of growth and development than are many other traits. The production of any specific shape must require a highly coordinated control over growth, but the means by which such control is exercised are quite beyond our present knowledge. Shape traits are probably no more complex in character than others, but they do bring us more directly to the fundamental problem of how a gene can determine the production of a specific character. They possess an advantage over most traits for a study of this problem in that all stages in the development of such a trait can be observed directly. A merely descriptive study of development is evidently very far from an adequate analysis of the process but even such a meagre basis of fact is worthy of careful scrutiny in a field where all is still so obscure. Investigation of the development of a structure with a given shape in material where this shape has been analyzed genetically is therefore of value in offering a possible clue as to the method of genetic control.

The development of fruit shape provides exceptionally favorable material for studies of this sort since the entire course from the minute primordium of the ovary to the mature fruit, many thousands of times as large, may in most cases be readily followed, and since in a number of genera fruit shape has been subjected to a rather thorough genetic analy-

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sis. The senior author (1929) has already described the developmental changes in various types of *Cucurbita Pepo*. In this species the wide diversity in shape in the mature fruits of different varieties is already evident in very small ovary primordia. The very elongate forms, the spherical ones, and the flattened or disk types are distinguishable as such in the youngest stages which can be measured.

Much more material of this species has recently been studied and has been analyzed according to the method suggested by Huxley (1932) and others, which eliminates the disadvantages of employing a ratio or index of dimensions as a measure of shape characters. Instead of comparing the actual size of the two dimensions studied at successive periods or determining their relative growth rate in terms of *actual* growth, this method ascertains their relative growth rate more accurately by using proportional increase (increment divided by size) as a measure of growth. Thus, essentially, the "compound interest" rates at which the two dimensions are growing are compared. This can readily be done by plotting the dimensions studied (commonly length and width) logarithmically. Their relation to each other and any changes in it may now be ascertained independently of the actual size of either.

In a growing structure the character of the line thus formed indicates very simply any alterations which may occur in relative growth in the two dimensions and thus in the shape of the structures produced. If there is no change during development this line will be straight and will have a slope (as normally plotted) of 45°. If there is any consistent and progressive change in this relationship, the line will also be straight but will have a greater or lesser slope depending on which dimension is growing faster relative to the other.

Huxley has presented a formula for the determination of this relative growth rate and thus of the slope of the line when dimensions are plotted logarithmically. If y is one dimension (length, let us say) and x the other (width), then the relation between them at any point is $y = bx^k$, where b is a constant, the initial difference between length and width (or the value of y when $x = 1$), and where k, another constant, is the ratio between the growth rate (proportional or "interest" rate) of length divided by that of width. Where length and width are increasing at the same rate, $k = 1$. If length is growing faster than width, k will be greater than 1 and (if length is plotted vertically) the line will slope upward more steeply; if width is growing the faster, k will be less than 1 and the line will be more nearly horizontal. Differences in the relations between length and width (and thus in shape) may therefore be due to differences in either the value of b or the value of k.

When measurements were made in *Cucurbita* of the length (polar diameter) and width (equatorial diameter) of ovary primordia and fruit

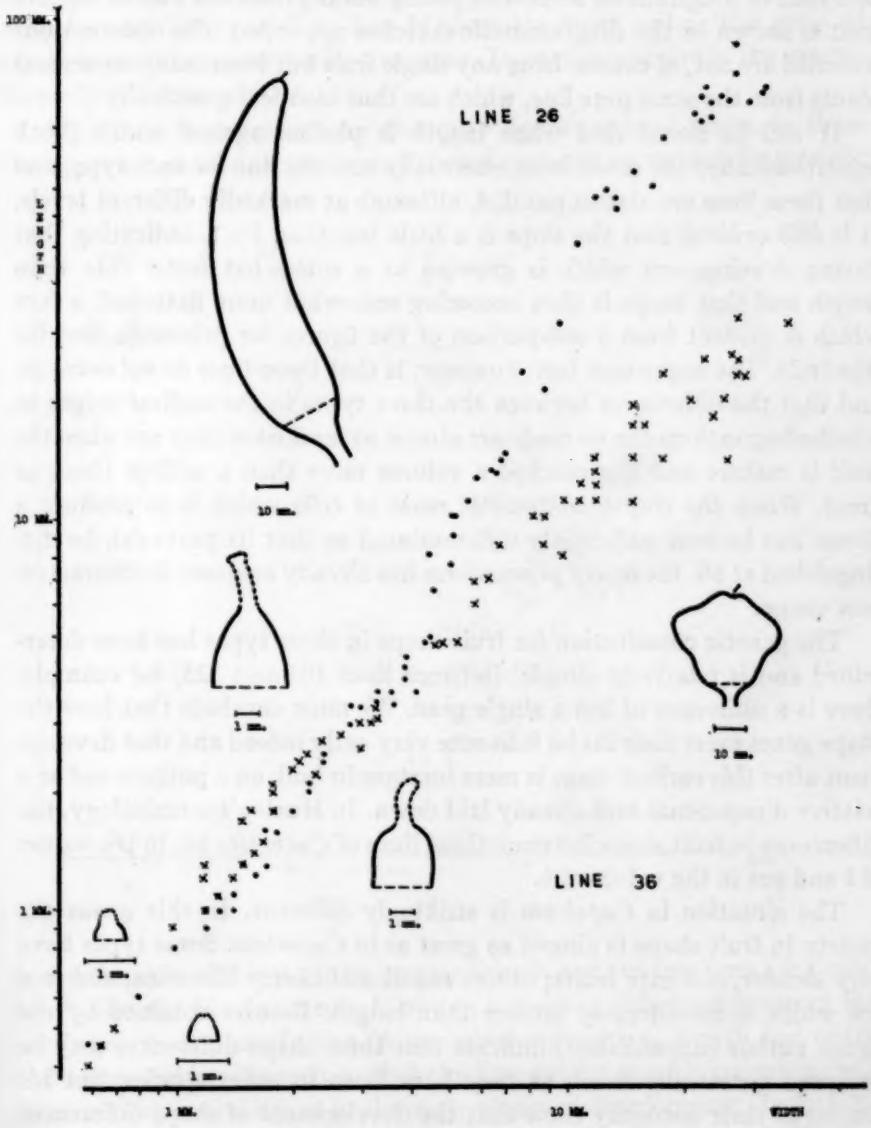

Fig. 1.

in all stages from the earliest ones observable until maturity in three lines differing markedly in fruit shape, and when each measurement was plotted logarithmically, the results shown in figure 1 appeared. Line 6 has a much

elongated fruit, line 103 an essentially spherical one, and in line 125 width is much greater than length, producing a flattened or disk fruit. The appearance in longitudinal section of young floral primordia and of mature fruit is shown in the diagrammatic sketches appended. The observations recorded are not, of course, from any single fruit but from many on several plants from the same pure line, which are thus identical genetically.

It will be noted that when length is plotted against width (both logarithmically) the result is an essentially straight line for each type, and that these lines are almost parallel, although at markedly different levels. It is also evident that the slope is a little less than $k=1$, indicating that during development width is growing at a somewhat faster rate than length and that shape is thus becoming somewhat more flattened, a fact which is evident from a comparison of the figures for primordia and for ripe fruit. The important fact, however, is that these lines *do not converge*, and that the differences between the three types in the earliest stages at which observations can be made are almost as marked as they are when the fruit is mature and has reached a volume more than a million times as great. When the tiny meristematic mass of cells which is to produce a flower has become sufficiently differentiated so that its parts can be distinguished at all, the ovary primordium has already assumed its characteristic shape.

The genetic constitution for fruit shape in these types has been determined and is relatively simple. Between lines 103 and 125, for example, there is a difference of but a single gene. We must conclude that here the shape genes exert their major influence very early indeed and that development after this earliest stage is mere increase in bulk on a pattern and at a relative dimensional rate already laid down. In Huxley's terminology, the differences in fruit shape between these lines of *Cucurbita* are in the values of b and not in the values of k.

The situation in *Capsicum* is strikingly different. In this genus the variety in fruit shape is almost as great as in *Cucurbita*. Some types have very slender, elongate fruits; others round and cherry-like ones, and in a few width is considerably greater than length. Results obtained by the junior author (unpublished) indicate that these shape differences may be analyzed genetically much as they have been in other species, but his studies of their ontogeny show that the development of shape differences here is radically different from that described above for *Cucurbita*.

In figure 2 a comparison is presented between two types of *Capsicum* fruit. Line 26 has, at maturity, a very elongate, pointed fruit. In line 36 width and length are approximately equal, though the fruit is not spherical because of the presence of an equatorial ridge. Marked as are the

differences between these two fruit types at maturity, they are almost absent at the time of flowering. The middle diagrams for each line represent the longitudinal profile of the ovary at anthesis. Except for a somewhat broader "shoulder" in line 36 they are much alike. The ratio of length to width is practically the same. In earlier primordia the resemblance is still more clear.

When length and width for the early developmental stages in these two types are plotted logarithmically, each presents an essentially straight

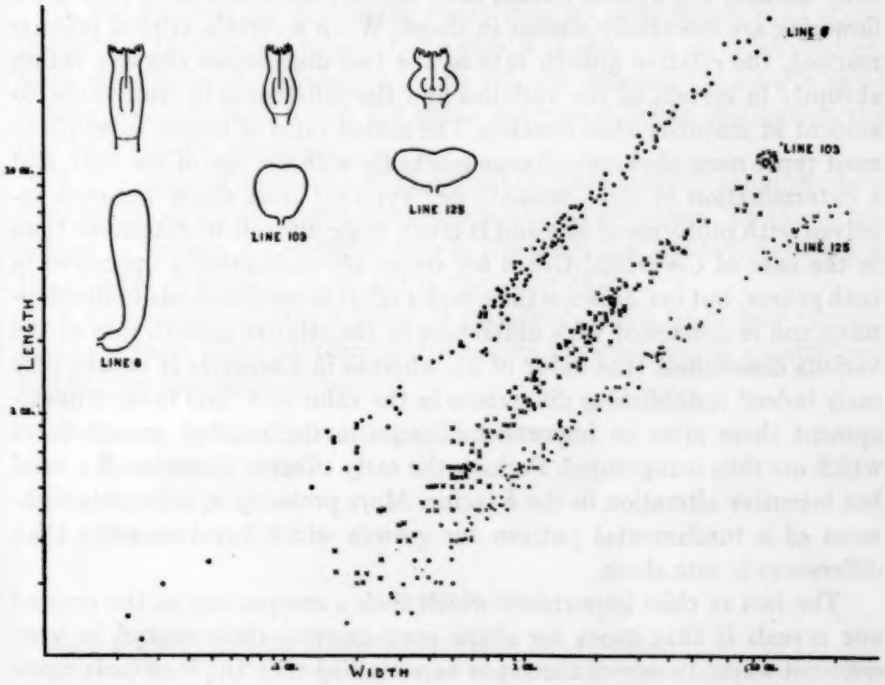

Fig. 2.

line with a value for k of a little greater than 1, and the two lines are superposed. Shortly after anthesis, however, a marked difference between the two begins to appear. In line 36 the relative growth of length and width maintains itself unchanged so that the line continues with approximately the same slope established in the early stages of development. In line 26, on the other hand, the line slopes upward steeply and abruptly, indicating the length has now begun to grow at a considerably faster rate than width. It should be understood that this difference is not only in actual rate but in true or proportional rate, as though length were now growing at a higher "rate of interest" than width. As a result of this difference the

elongate fruit shape begins to emerge. Shortly before maturity, relative length growth drops again and the slope of the line is once more not far from $k = 1$.

It is evident that in *Capsicum* the major effects of the differences in genetic constitution for fruit shape are not produced very early in development, as is the case in *Cucurbita*, but appear only after a relatively late stage has been reached. Certain minor differences in outline are evident even before anthesis, but in all of the widely diverse varieties which have been studied, the ovaries during early development and for a time after flowering are essentially similar in shape. When a certain critical point is reached, the relative growth rate of the two dimensions changes rather abruptly in certain of the varieties and the differences in fruit shape so evident at maturity thus develop. The actual ratio of length to width in most types must obviously change markedly with the size of the fruit, and a determination of the "normal" or "typical" fruit shape becomes involved with problems of size and is much more difficult to determine than in the case of *Cucurbita*. Genes for shape are undoubtedly operative in both genera, but in *Capsicum* their major effect is produced late in development and is concerned with differences in the relative growth rate of the various dimensions (the value of k), whereas in *Cucurbita* it occurs very early indeed (establishing differences in the value of b) and in later development there arise no important changes in the relative growth rates which are thus inaugurated. Perhaps the early effect in *Cucurbita* is a brief but intensive alteration in the k factor. More probably it is the establishment of a fundamental pattern for growth which involves more than differences in rate alone.

The fact of chief importance which such a comparison as the present one reveals is that genes for shape may exercise their control in very different ways. In one of the types here studied they impinge early upon the developmental cycle and set up different levels of relative growth which are thereafter maintained with little modification. In the other, they seem to impinge at a much later stage and to produce their effect through a modification at that time of the growth rate of one dimension relative to that of the other. Of course in both cases shape genes must be present from the very beginning of development, and they may well be active in performing their critical rôles long before the effects of this activity are externally evident. The fact that there are such marked differences in the time of visible gene effect, however, suggests that a more detailed analysis of such divergent types may throw some light on the general problem of the relation between genetic constitution and developmental processes.

SUMMARY

1. Developmental stages from the youngest observable ovary primordium to mature fruit were studied in pure lines, differing in fruit shape, of *Cucurbita* and *Capsicum*. Length and width were both plotted logarithmically for these stages.

2. In *Cucurbita* the various shape types are visible in the earliest primordia and the relative dimensional growth rates there established persist essentially unchanged to maturity.

3. In *Capsicum* the developing ovary from its early stages until about the time of fertilization is essentially similar in shape in all types studied. Soon after anthesis, differences in the relative dimensional growth rates appear, as a result of which the shape differences which distinguish the mature fruits are produced.

4. The stage of development at which the genes for fruit shape produce their visible effect thus differ markedly in these two genera. In the terminology of Huxley, shape differences in *Cucurbita* are due to differences in the value of *b;* those in *Capsicum*, in the value of *k*.

5. It is suggested that a study of such contrasting types may provide results of value in the problem of the relation between genetic constitution and developmental processes.

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The archegonia of Pellaea viridis (Forsk.) Prantl

W. N. Steil

When the writer (1915) reported apogamy in *Pellaea viridis*, he stated that archegonia were observed to develop on about fifty per cent of the prothallia. These sex-organs never exceeded four in number on any of the many prothallia examined. The archegonia appeared normal in every respect, and when they opened, attracted the antherozoids in large numbers. As a result of an examination of stained sections of the archegonia, no abnormal development of the egg was observed. Whether embryos develop as a result of fertilization has not been determined.

The archegonia in *Pellaea viridis* are produced, as is usual in the ordinary homosporous leptosporangiate ferns, back of the apical notch and on the well developed cushion. In this region the embryo of apogamous origin develops.

When the prothallia of *Pallaea viridis* were grown in subdued light, plates of irregular form usually consisting of a single layer of cells, and branching filaments were produced in large numbers.

In the absence of typical heart-shaped prothallia, characteristic of this species of fern, apparently normal archegonia were produced on plates and filaments which were formed in the subdued illumination.

Figure 1 represents a prothallium of *Pellaea viridis* grown for a short time in subdued light. One of the wings of the gametophyte, which had already assumed a heart-shaped form when grown in favorable light, produced in the weaker illumination a narrow plate one cell layer in thickness from which later a filament of a single layer of cells was produced. It will be observed that the filamentous portion formed a plate again, a part of which became considerably thickened. On this portion two archegonia developed. In this region the cells are considerably smaller than those in other portions of the gametophyte. The presence of small cells and the short filament of five cells, originating from this meristematic region, are evidences for the fact that an embryo of apogamous origin is beginning its development. Toward the growing end of the gametophyte, have been produced numerous short cells the walls of which for the most part are approximately parallel to one another. These cells, it is obvious, are not typically gametophytic. Such filaments have been frequently observed in the gametophyte of other apogamous ferns. In fact, cells of this nature are of common occurrence in the tongue-like outgrowth of the apical notch of the gametophyte of some apogamous ferns.

Archegonia were sometimes observed to develop on filaments consist-

ing of a single layer of cells (fig. 2). It is observed in this instance that there is a sharp line of demarcation between the cells of the filament and those of the plate.

The archegonia were frequently produced on plates composed of a single layer of cells (fig. 3). The gametophyte in this instance has also formed a filamentous portion composed of peculiar cells of regular form and which are usually associated with an embryo of apogamous origin. This portion, however, of the gametophyte is removed some distance from the archegonia.

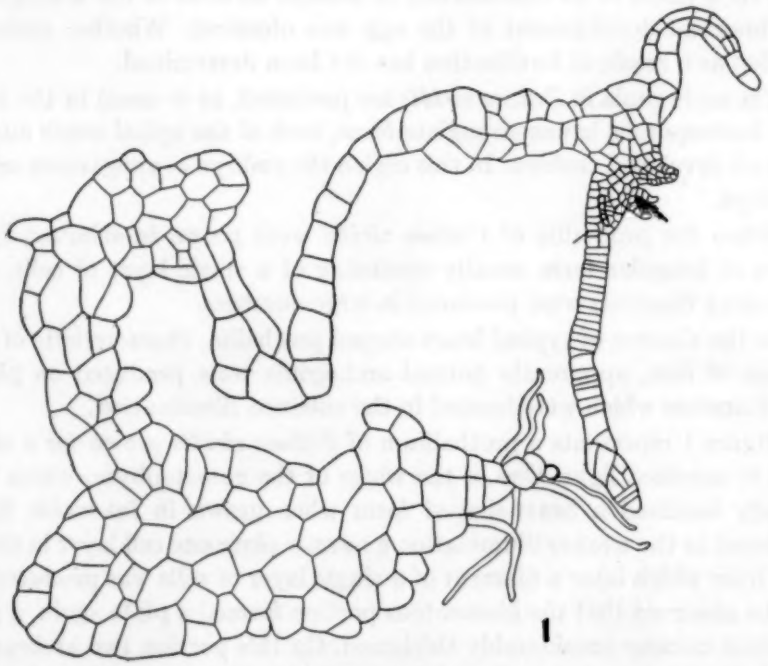


Fig. 1. A gametophyte of *Pellaea viridis* from one of the wings of which plates and filaments have been alternately formed. Archegonia and an early stage in the development of the apogamous embryo shown.

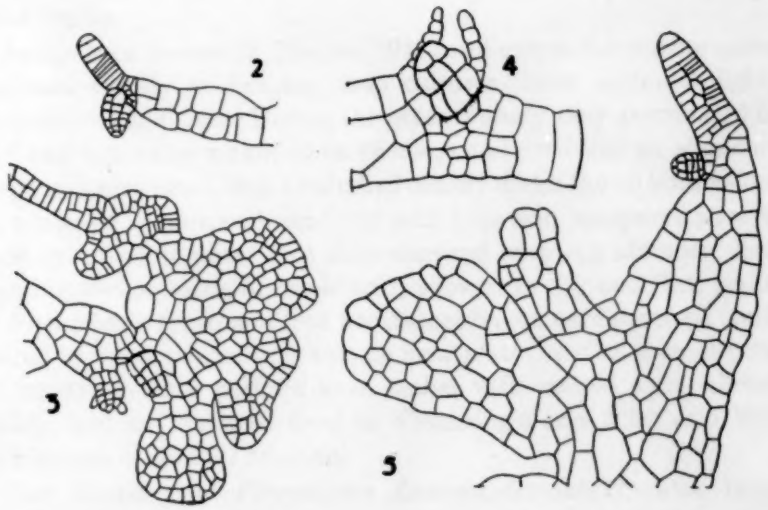
In some instances the archegonia were produced on thickened portions of plates, as is shown in figure 4. Their development was not associated in this case with an embryo of apogamous origin.

Archegonia were observed also to develop on the lobes or wings of the prothallium (fig. 5). In some instances, however, archegonia were associated with an embryo produced apogamously.

These observations made on the development of the archegonia of *Pellaea viridis* are of interest since the archegonia in the ordinary homo-

sporous leptosporangiate ferns are produced on the cushion of the gametophyte and where antheridia are not commonly formed. The writer (1919) however has reported in *Pteris ensiformis* var. *Victoria* the presence of numerous antheridia on the cushion. They completely surround the archegonia.

In the *Polypodiaceae* no one has previously reported, so far as the writer is aware, the development of archegonia on plates and filaments of the gametophyte and which have been described in species of *Trichomanes* by Bower (1888) and Goebel (1898–1901), in *Hymenophyllum* by Prantl (1875) and Sadebeck (1889), and in *Schizaea* by Britton and Taylor (1901) and by Thomas (1902).



Figs. 2–5. *Pellaea viridis*. 2. A portion of the gametophyte showing the formation of archegonia between a plate and a filament. 3. A portion of a gametophytic plate composed of a single layer of cells and on which archegonia have been produced. 4. Archegonia produced on a cushion like portion of a gametophytic plate. 5. Archegonia produced on the lobe or wing of the gametophyte.

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Multiciliate zoospores in Physoderma Zeae-maydis

ELIZABETH OJERHOLM

The zoospores of *Physoderma Zeae-maydis*, a chytrid which causes serious damage to corn, have been described by Shröter (1889), Tisdale (1921), and others as being universally uniciliate. In the course of a cytological study of this organism during the past year, however, occasional biciliate and triciliate swarmspores were observed. In view of the bearing which such structures have on the problem of sexuality among the Chytridiales a more thorough investigation of the zoospores was undertaken to determine the origin of this multiciliate condition and its relation to sexual fusion.

As has been shown by Tisdale (1921) and others the resting sporangia germinate readily in hanging drop cultures under optimum light and temperature conditions. During the present study they germinated in distilled and tap water within 30 to 48 hours and produced an abundance of zoospores which could thus be studied readily under the oil immersion lens. For study of the nuclear condition and behavior, zoospores were transferred in a film of water to a slide smeared with egg albumen, fixed by inverting over a bottle of osmic acid, allowed to dry and then stained in the Flemming's triple and iron haematoxylin stains. Sporangia were also planted in water in small pockets on agar plates, and as soon as germination occurred these pockets were sealed with melted agar, allowed to solidify, and cut out and fixed in Flemming's and Allen and Wilson's modification of Bouin's solution.

The zoospores of *Physoderma Zeae-maydis* are liberated from the sporangium in rapid succession one after another or sometimes in small groups through an opening in the endosporangium wall. Approximately thirty have been counted in single sporangia, but because of their rapid exit and hyaline color, it is difficult to make an accurate count. When first liberated the zoospores swim away with a jerky motion, darting about among the sporangia; but gradually movement becomes more uniform, and they swim with a swift gliding motion. Ordinarily, the zoospores move swiftly from the field of observation in a direct line, but they may also frequently come to rest abruptly and then dart off rapidly in another direction. In rare instances the entire mass of zoospores has been found to come to rest at the mouth of the sporangium and soon degenerate without any motile stage. Whether this condition is due to immaturity or lack of cilia is not yet certain.

The uniciliate zoospores vary considerably in size and shape. While

active they are usually ellipsoid in shape, somewhat pointed at the anterior end, and vary from $3\times4\mu$ to $5\times7\mu$. The cilium is attached at the posterior end and is usually four to five times the length of the spore body. In the center of the zoospore is a prominent refractive body which often appears to lie in a vacuole with one or more smaller granules. This globule has been frequently observed to shift in position when the swarmspore is in rapid motion. Quite often it protrudes somewhat at one side, as has been described and figured by Tisdale. When xylol is drawn under the cover slip the refractive globule gradually disappears and leaves behind an indefinite granular mass. A similar change occurs by treatment with ether and chloroform, and in osmic acid the globule turns black. In preparations fixed in the ordinary solutions containing acetic acid it is lacking altogether, and a large vacuole is usually present in the space it formerly occupied. The reaction of the refractive globule to these various reagents thus indicates its fatty or lipoidal nature.

According to my observations the period of motility lasts for several hours, but I am yet uncertain as to the approximate time limit. In many hanging drop cultures motility has lasted for twenty-four hours, but this may be due to delayed germination of certain sporangia. All sporangia do not germinate at the same time, and it is highly probable that the continued motility in hanging drop cultures noted above is due to this fact. Isolation and germination of single sporangia for the solution of this question has not yet been made. During the motile period the zoospores often exhibit amoeboid movements, assuming various shapes. They may put out pseudopodia at the anterior end and sides and creep slowly with the cilium trailing behind. Often, however, they may swim rapidly away with the projecting pseudopods. Quite frequently they may become attached to the substratum by their pseudopods, and in such cases they may break loose by a vigorous shaking movement and dart rapidly away. Eventually the zoospores become more sluggish in their movement, somewhat spherical in shape, and lose their cilia. Often before coming to rest, however, they may swim around in circles and revolve on their own axes.

Frequently, as has been noted before, biciliate zoospores were observed swimming among the uniciliate forms. These are usually twice the size of the latter and have two cilia of approximately the same length attached at the posterior end. In some cases they appear to originate at the same point, while in others they are slightly separated. Thousands of zoospores have been studied in the living condition, but fusion between uniciliate individuals has not yet been observed. Two somewhat amoeboid-shaped individuals have frequently been seen to come in contact, undergo further amoeboid movements, and move off together but eventually sepa-

rating. Even in the actively motile condition two zoospores may come in contact, become entangled with cilia and swim around in this manner, but in no instance has actual fusion been observed.

In fixed and stained preparations approximately one per cent of the zoospores are biciliate. They usually contain two nuclei lying in close proximity to one another, but several individuals have been found with a single nucleus, approximately twice normal size. It seems thus that this nucleus may probably have arisen from the fusion of two nuclei. Between and somewhat above the nuclei is a large vacuole, apparently the region occupied by the refractive body in the living condition. Somewhat cone-shaped regions of dense fibrous cytoplasm extend from the nuclei to the points on the periphery of the zoospore where the cilia are attached. In this region lie several small granules. The structure of these zoospore is very similar to those of the Blastocladiaceae described and figured by Kniep (1929) and Barret (1912). In most fixed and stained preparations a large number of zoospores were found lying side by side and also overlapping to the extent that no definite boundary could be seen separating them, and at first sight it appears as if numerous stages in the process of fusion were present. However, in view of the fact that fusion has not yet been observed in living material it is perhaps premature to interpret these stages as such.

However, one case of fusion between a biciliate and uniciliate zoospore has been seen. The zygote thus formed subsequently exhibited numerous amoeboid movements for approximately an hour. The cilia remained separate and intact during the various changes in form, disappearing only after the zygote rounded up and came to rest. Several triciliate zoospores have also been found in fixed and stained preparations. A similar case of fusion between a large biciliate zoospore and a smaller one has been described by Wilson (1920) in *Urophlyctis alfalfae*, which he interprets as evidence of heterogamy. Sufficient evidence, however, has not yet been found to warrant such a conclusion for *Physoderma Zeae-maydis*. Copulation between motile gametes dissimilar in size and shape has also been described for *Allomyces javanicus* of the Blastocladiaceae by Kniep (1929).

As to the origin of the tri- and biciliate zoospores described above in *Physoderma Zeae-maydis* there are, it seems to me, in general two possibilities: (1) fusion between zoospores or gametes and (2) abnormal, unequal or incomplete cleavage. Although actual fusion has been seen only in one instance, the first probability is, nonetheless, supported by evidence from other chytrid species. Fusion of zoospores or motile isogametes has been reported by Sorokin (1874) for *Tetrachytrium*, Fisch (1884) for *Reesia* and *Chytridium mesocarpi*, Woronin (1878) for *Olpidium brassicae*, Dangeard

(1889) and Chatton and Brodsky (1909) for *Sphaerita*, Lowenthal (1905), Kusano (1928, 1930) and Curtis (1921) for *Synchytrium*, Doflein (1907) for *Nucleophaga*, Kusano (1912) for *Olpidium viceae*, Wilson (1920) for *Urophlyctis*, Couch (1931) for *Micromyces zygogonii*, Swartz and Cook (1928) for *Olpidium radicale*. Köhler shows fusion between two uniciliate gametes and also between three uniciliate gametes in *Synchytrium endobioticum*, thus forming bi- and triciliate zygotes. Such fusion between three gametes has also been described among the algae by Geitler (1931) for *Tetraspora lubrica*. Among the Blastocladiaceae fusion of motile gametes has been reported by Kniep (1929) for *Allomyces javanicus*. Fusion has also been reported to occur in the parasitic slime moulds by Cook (1931) for *Sorodiscus radicicolus*.

On the other hand, the view that the multiciliate zoospores are abnormal and have arisen through unequal and incomplete cleavage is likewise supported by evidence in the literature. In *Olpidium viceae* Kusano (1912) found abnormal multiciliate zoospores which he interpreted as having originated from incomplete cleavage. Lagerheim (1889) likewise figures abnormal bi- and triciliate zoospores in *Olpidiella uredinis*. In the algae also, large four ciliate zoospores resulting from incomplete cleavage have been reported by Wille (1887) for *Trentepohlia umbrina*. Going to the Oomycetes, zoospores with one, two, and three cilia have been described for *Pythiopsis* by Coker (1914). In *Isoachlya unispora* Coker (1923) figures double spores with four cilia and also masses of protoplasm which have escaped from the sporangium without forming into spores. Cotner (1930) also figures four-ciliate giant spores in *Saprolegnia monoica var. glomerata*. Since *Saprolegnia* and *Pythiopsis* are definitely heterogamous with nonmotile antheridia and oogonia these spores have no significance from the standpoint of sexual fusion, and are doubtless abnormal. According to Cotner zoospore formation is dependent to a great degree on temperature, and the giant zoospores in *Saprolegnia* are formed as the result of unfavorable temperature conditions. Kniep also finds giant triciliate zoospores in *Allomyces javanicus* which are formed as a result of incomplete cleavage. This form then, supports both contentions as to the origin of the multiciliate zoospores. In view of this data the multiciliate zoospores observed in *Physoderma Zeae-maydis* may possibly be the result of incomplete cleavage due to unfavorable temperature conditions, since no attempt has been made in this study to control the temperature.

There is thus evidence in the literature supporting both of these viewpoints, and until further data are at hand, it would be premature to say whether or not the multiciliate zoospores observed in *Physoderma Zeae-maydis* are entirely the result of fusion or incomplete cleavage. A further

study of this problem is now in progress and will be reported in another paper on the cytology of this parasite.

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The rate of growth of the ponderosa pine in Estes Park, Colorado

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A study of the ponderosa pine, formerly known as western yellow pine (10), *Pinus ponderosa* Dougl., and its varieties, in its range from north to south and from east to west would lead one from British Columbia to lower California and northern Mexico, and from the Pacific coast to central Nebraska. Within this range *Pinus ponderosa* is found on fertile, moist mountain slopes, on dry rocky ridges in the midst of granite and limestone outcrops and cliffs, in fertile valleys, and on dry arid slopes of the mountains and foothills. The highest outposts are found above 9000 feet of elevation in the central Rocky Mountain region and the lowest ranges are in the northern Sierra Nevada of California and the river valleys and canyons of Nebraska at about 2500 feet. Its rate of growth in a range as great as this presents many extremes under great variations of light, temperature, precipitation, and soil moisture.

Average growth rates have been determined by comparing and contrasting trees growing in stations which present conditions of similar and comparative nature. It is the purpose of this paper to present findings as to growth rate of *Pinus ponderosa* within the area studied. The effects of mistletoe infection, of lightning damage, and observations of bark beetle injury are also noted in their relation to growth rate of the ponderosa pine.

The data were obtained within a radius of ten miles of the village of Estes Park, Colorado, except one extreme which led down the Big Thompson canyon to within a few miles of Loveland, Colorado. This places one in the eastern division of the central Rocky Mountains and is considered by some as a transition zone from north to south. With this as a location the rates of growth presented can favorably be compared with those found in mountainous regions north, west and south and with the plains or valley regions to the east.

The ponderosa pine was found growing in this area at elevations ranging from 5200 feet to 9700 feet. These, however, are the extremes and the usual range is from 6000 feet to 8500 feet. Within this range of elevation the species is found in purest stands on the south slopes. This indicates the well known fact that the ponderosa pine is capable of growing in warmer and drier situations than the other conifers of the same range.

As one goes from the south to the west slope more and more Douglas fir, *Pseudotsuga taxifolia*, is found, until on the north slope one often finds an almost pure stand of this species. From south to east this transition is more rapid than from south to west due to a more abundant moisture supply on the east slopes.

The virgin stands of ponderosa pine are very uneven-aged due to the natural succession (11). The species, growing as it does primarily in the arid portions of the area, is free from competition with other species on account of its extreme intolerance. Thus, the seedlings become established in the openings as they occur by the death or removal of the older trees and ponderosa pine follows ponderosa pine. Other species may enter but not as permanent invaders and the ponderosa pine is free to succeed itself. Aspen groves are found locally in moist sites but these are small in area, the trees are few and usually retarded and so cannot be considered important as a stage of succession. When the ponderosa pine is found growing in mixed stands, it seems to hold its own or in some cases to increase its percentage to a limited degree (5).

METHODS

The data were obtained from ten localities within the above area. All trees were measured in two localities, one a typical south slope, and one a typical west slope; while in the other localities type trees were selected at random merely as average specimens. The following data were recorded for each tree:

(1) Height. This was obtained in feet by the use of the Faustman hypsometer.

(2) Diameter. This was determined mathematically by measuring the circumference with a steel tape. All diameter measurements were taken in inches breast high, approximately four and one-half feet from the ground.

(3) Growth. Cores were taken from each tree by use of the Swedish increment borer. In all cases the cores were taken from north and south radii at the same height as the diameter measurement. The most important data were secured from these cores. By the use of a binocular microscope the annual rings were marked off in ten year periods. These periods were then measured in millimeters and recorded on work sheets for further comparisons. A total of 236 trees were included in securing data.

(4) Altitude. In order to locate extremes and to make more definite comparisons the altitudes were recorded at the various stations by use of an anaeroid barometer.

(5) The type and general appearance of each tree was noted.

(6) The general habitat for each tree or group of trees was recorded in field notes.

STATIONS

Since the ponderosa pine is found in purest stands on the south slopes, the most intensive observations were carried out on these typical areas.

A slope of virgin forests on Olympus Heights, which extends from Mt. Olympus, is typical of the ponderosa pine forests of the area. The elevation of this station ranges from 7525 feet at the base to 7950 feet at the top.

Although the south slope forests are often considered a pure stand of ponderosa pine, a few other species are found. On the upper part of the slope a few Douglas fir are found, but compared to the ponderosa pine, over the entire area, they are present only in a ratio of 1 to 21. Western cedars, *Juniperus monosperma*, are scattered all along the slope and many of them are able to exist in very dry situations. The sprawling juniper,

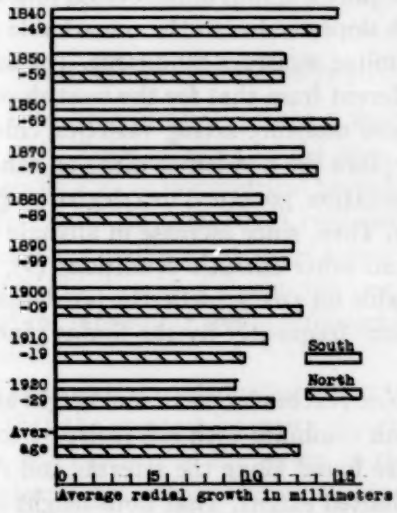

Fig. 1. A comparison of the north and the south radial growth of 95 trees under 100 years old, ring count breast high.

Juniperus communis, although not a tree, is also present. A few aspens are found, but these are small and grow only in the protected and moisture-holding coves.

The shrubs most common on this south slope area are *Purshia tridentata*, *Jamesia americana*, and one or more species of *Ribes*. Open areas 50 to 150 feet or more in diameter are often found where only shrubs and scant herbaceous growth is present. These open areas generally include much exposed rock and very shallow soil in which ponderosa pines have failed to become established.

After careful observations, a typical west slope was selected about a mile from the south slope station. The range of elevation for this slope is from 7650 feet to 8125 feet. In addition to the ponderosa pines an average of 82 douglas fir were found to the acre in the west slope station. The total

average, including a few limber pines, *Pinus flexilis*, and the junipers, was 180 trees to the acre. In contrast to this, only 106 trees were found to the average acre on the south slope. As one observes the transition from a south to a west or east slope, the change from an open to a more dense forest type is readily noted. This transition continues in this marked degree until the densest forests of the lower elevations are found on the north slopes. With this marked change in number and type of trees from south to north slope there is also noted a corresponding increase in depth of soil and the amount of humus that is retained on the surface.

The fact that the purest stands of ponderosa pine are found most abundantly on the south slopes is due to the remarkable ability of the species to adjust itself to limited moisture conditions. The actual number of trees per acre is little different from that for the west slope but moisture is not sufficient for the more moisture-loving varieties, chiefly Douglas fir. The latter are able to replace the ponderosa pines on other slopes of the same elevation since evaporation, governed to a degree by prevailing wind direction, is not so great. Then, since increase in altitude usually brings an increase in rainfall, and other climatic conditions (9), chiefly temperature, are also more favorable for tree growth, the ponderosa pines are displaced on higher slopes, more frequently by the limber pine, Englemann spruce, or alpine fir.

The ponderosa pine reaches its maximum height and diameter development when soil depth combines with soil moisture to make ideal growing conditions. These are found along the streams and rivers in areas which, as a rule, are of a limited extent. That both height and diameter growth are accelerated by water supply is shown by comparing trees growing in moist favorable situations with trees growing in dry situations. To make this comparison 89 trees under 100 years of age, ring count breast high, were studied in fourteen stations based upon three classifications; moist,

TABLE 1

A comparison of diameter growth in millimeters of trees under 100 years old, breast high measurements, divided as to habitat; moist, medium, and dry

DECADES		1920-29	1910-19	1900-09	1890-99	1880-89	1870-79	1860-69	1850-59	1840-49	DECADE AVE.
REGION	NO. OF TREES										
Dry	25	11.7	13.9	16.05	19.6	20.9	21.7	19.6	17.6	20.1	17.9
Medium	48	18.9	22.3	21.9	23.5	22.5	29.1	20.5	28.5	33.7	24.54
Moist	16	39.6	40.3	47.9	55.3	42.5	38.5	48.0	35.0	43.3	43.37
Average		23.4	25.5	28.62	32.2	28.63	29.77	29.37	27.03	32.37	28.61

medium and dry. Those growing along streams and rivers were considered growing in moist habitats, those of the higher dry slopes, both west and south, as dry, and those between, of a medium range. The average diameter contrast for moist and dry situations is evident enough to show a great advance in diameter growth where water is available. The trees of medium range are related, as far as diameter growth is concerned, more closely with the trees of the dry habitat. The comparative diameter average per decade as based on core measurements was 17.9 millimeters for the dry, 24.6 millimeters for the medium, and 43.4 millimeters for the moist habitats. Comparisons of diameter growth per decade in millimeters are made in table 1.

FORM AND ECCENTRIC GROWTH

It is well known that density of stand has a marked effect upon the general form of the tree. Trees growing in the open develop a broader, lower crown and generally a more symmetrical branching effect. The slope also has a marked effect upon the form of the tree. On the down slope side the branches are often lower and in many cases longer, thus, in these cases the larger per cent of the food making area of the tree is on the down side. Steepness of slope and the immediate tree environment are both modifying factors of this condition.

Light is probably the greatest contributing factor to the unsymmetrical crown. It is evident that the greatest intensity of light is from the south, thus, the responsive development of the crown in this direction. Only a per cent of the ponderosa pines have extremely unsymmetrical crowns and not all of these are heaviest on the south. Further, there seems to be a direct relation to slope as well as to light. Of 25 trees on the south slopes all of which showed one-sided crowns, 20 were most heavily branched on the south, the others showed inclination to the west and one to the east. On the west slope this proportion was not quite so high and the balance here was as much toward the downhill side (west) as toward the south. It is evident that practically all of the one-sidedness throughout the range is to the south, southwest, or west and proportionately in this order. Wind may enter as a factor but to a minor degree since the ponderosa pine habitat is more or less protected. The chief factors influencing the balance of the ponderosa pine branch-leaf arrangement are light and slope.

Associated with the unsymmetrical crown is the eccentric growth of the bole of the tree. In a major portion of the ponderosa pines of this area growth is greatest on the north side. With some of the trees one could easily assume that a direct food relation existed. Büsgen and Münch (4) however, disprove this by an experiment of defoliation and conclude that it is a

difference in tension on the different sides of the shoot. This conclusion also agrees with Behre (3), with the exception that he considers the probability of effect which a minimum and suppressed distribution of foliation could bring about.

In order to compare the general ratio that exists between the north and south radii, the increments from these respective sides were averaged and compared. As can be noted in figure 1, the total average per decade is not constant. In four decades out of the nine, the balance was to the north, in five to the south. The average for all decades was slightly to the north.

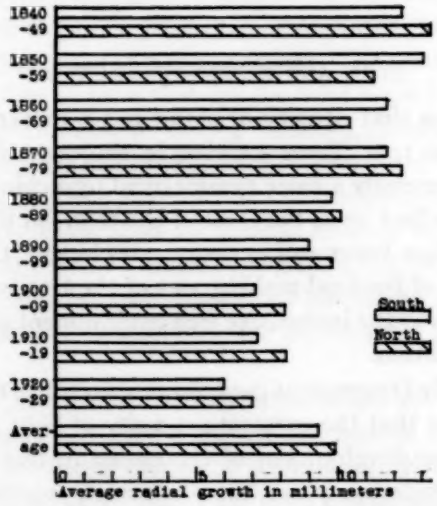

Fig. 2. A comparison of the north and south radial growth of 38 trees growing on a south slope.

This comparison is shown better in figure 2 in which 38 trees growing on a south slope were selected to compare north and south radii. The trend toward a greater north radius is more definite, thus showing that slope is an important factor. All decades except two, those in the early life of the tree, show an advance of north over south in the radial growth. The graph represents the total growth as the trees selected for this comparison were all less than 100 years old.

A numerical comparison of the north and south radial growth is made in table 2. Here also diameter comparisons are made. The minimum and maximum radial and diameter growth for individual trees per decade from 1840 to 1929 are made in this table. The minimum radial growth is found most abundantly on the south while the maximum for the north and south are about the same, averages considered. That light inhibits growth

TABLE 2

Growth data in millimeters on trees under 100 years, total ring count breast high. Average 64.9 years

DECADE	1920-29	1910-19	1900-09	1890-99	1880-89	1870-79	1860-69	1850-59	1840-49	DECADE AVE.
North Radius										
Maximum	31	39	39	50	30	30	32	33	21	33.9
Average	11.82	10.26	13.3	13.03	11.8	14.23	15.43	12.5	13.57	12.88
Minimum	1.15	1.4	1.2	1.5	1.5	1.5	1.6	2.5	6.3	2.1
South Radius										
Maximum	35	31	39	41	41	32	32	24	30	33.9
Average	9.62	11.68	11.63	13.18	11.9	13.47	12.3	12.74	17.27	12.66
Minimum	1.2	0.8	1.2	1.2	1.8	0.7	1.0	2	8	1.2
Diameter										
Maximum	66	70	78	91	71	62	64	57	51	67.7
Average	21.44	21.94	24.93	26.2	23.7	27.7	27.73	25.24	30.48	25.54
Minimum	2.7	2.2	2.4	2.7	3.3	2.2	2.6	4.5	14.3	2.825*
Number of trees	95	95	87	83	68	56	40	27	14	

* Omitting 1840-49.

has been shown in the case of herbaceous stems in their adjustment to light, and could be assumed in the case of woody stems. Here we have a minimum growth on the south or down slope side and also the greatest light intensity, slope and shadows being considered in the latter.

THE OPEN STAND

The open nature of the ponderosa pine stands is prominent and the three outstanding factors which contribute to this condition are light, temperature, and moisture. The species is intolerant of shade and this is effective very early in the life of the tree. The seedlings do fairly well in the shade of the parent trees, but saplings do not thrive until they receive direct light. The most important temperature relations for establishment of the seedlings are found in the surface and near-surface soil layers (2). The continued temperature requirement of the sapling and thus of the tree is that of the air, correlated with the soil surface temperature. The water requirement is relatively high as compared to the other species of the region (1). Thus, the demand of the tree for moisture leads to root

competition for soil space when moisture is insufficient. Bates (2), has shown that even though the ponderosa pine requires much heat and light, hence the warm open slopes, that it does use comparatively large amounts of water per tree of a given size. The tree is able to establish itself in its site by prompt germination and a deep, rapid, rooting habit of the seedling. Following the establishment of a deep tap root the lateral roots are extended and the severest stages of competition are brought about. The seedling is not able to compete with the roots of established trees and is consequently crowded out. Thus, the establishment and perpetuation of the open stands of ponderosa pine are controlled by temperature, light, and moisture requirements.

BIOTIC FACTORS

There are many biotic factors which have direct bearing on the rate of growth of the ponderosa pine. The two of greatest economic importance in the area are the bark beetle *Dendroctonus brevicomis* and the mistletoe *Arceuthobium cryptopodum*. Fungous parasites are also numerous throughout the region but are beyond the scope of this paper.

The bark beetle attacks trees throughout the area and many trees are observed in dead or dying condition due to its ravages. It has been estimated (7) that about 2000 beetles will actually kill a tree, but when smaller swarms attack, the tree is usually able to protect itself. The adult beetles bore through the bark to the cambium and eggs are deposited in egg galleries. They hatch very soon and the larvae spend their feeding stage in the phloem region, gradually making their way into the outer bark, pass into the pupa stage and finally emerge as adults and repeat the life cycle.

Two annual attacks are made by a brood and its offspring each year; the first in June and July, and the second in August and September. Following the second attack the brood winters in the inner bark layers of the infected tree (7). That the action of the beetle is very vigorous is evidenced by the rapid yellowing of the leaves and complete death of the tree in about three weeks. The most effective control measure is the cutting of the infected tree and removing and burning the bark in which the larvae are embedded. Some control measures of this nature are being carried out in the Estes Park area. Even though the bark beetle kills many trees, others are able to withstand the attacks and survive. These survivals can be identified by the holes left in the bark by the ingoing beetles and quite often additional holes made by birds in aiding the tree in its fight against the invader.

Hopping (6) finds that trees struck by lightning are often the target of

beetles, especially in the case of an epidemic. Miller and Patterson (8) find that bark beetle attacks are stimulated by a light burn. It is thus seen that many factors aid in bark beetle attacks throughout the ponderosa pine forest and constant control measures are essential if the pest is to be controlled.

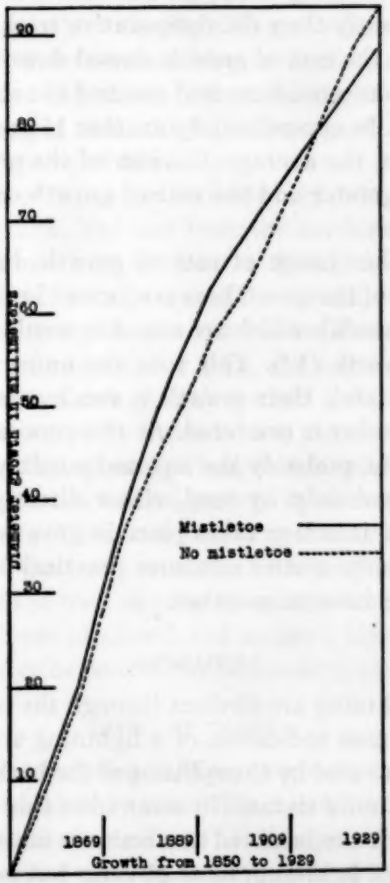

Fig. 3. To show the rate of growth of a group of trees affected by mistletoe as compared to a group free from mistletoe.

The ponderosa pine of this area is subject to severe injury by mistletoe. A tree infected by mistletoe very soon shows a decreased rate of height and diameter growth. The rate of decreased growth is directly in proportion to the severity of the infection. Accompanying this height and diameter decrease is a reduction of the leaf surface of the host. Gradually, then, the tree decreases its normal life functions and a slow death occurs (12).

The increments of five infected and five non-infected trees growing in an infected area are compared in figure 3. The trees selected were growing on the same slope in apparently similar conditions. The ages of the infected trees, according to ring count breast high, ranged from 69 to 93 years, an average of 77.4 years; the non-infected trees from 65 to 95 years, an average of 75.5 years. According to the growth curve, the infected trees were growing more vigorously than the comparative trees at the time of infection. After infection the rate of growth slowed down rapidly and in a ten year period the non-infected trees had reached the same diameter as that of the infected trees. In approximately another 15 years, at the time when the cores were taken, the average diameter of the non-infected trees was several millimeters greater and the rate of growth continuing to increase over the infected trees.

In addition to the change of rate of growth, brooms and burls are formed on the trunk of the tree. These are formed in the region of infection by using the food materials which are stored or would have been stored for the next seasons growth (12). This robs the outer branches and upper shoots of necessary food, their growth is much retarded and a striking distortion of the member is produced. As this process continues many of the outer branches die, probably the top, and possibly the entire tree.

Mistletoe is spread only by seed, either directly from the plant or carried by birds, and infection takes place in growth not more than four years old (13). The only control measures practical for an infected region is the removal of the infected member.

LIGHTNING

The effects of lightning are obvious through the ponderosa pine forest area. The most common indication of a lightning struck tree is an open scar down the trunk caused by the splitting of the bark by a current traveling down the moist, inner tissues. In some trees this scar has healed over and the remnants of it can be noted as a resinous mass in the tissues of the tree. Another effect of lightning, more obvious but not quite as common, is the "stag head." In the stag head the entire cambium region of the leader has been burned severely for a distance down the tree and as a result this portion of the tree dies. In addition to the stag head, a scar is usually formed down the trunk of the tree. In some cases the blast of the lightning bolt is enough to break off limbs or even to tear out the entire top of a tree.

Since a detailed study of the effect of lightning on an area cannot be made here, a study will be made of cores from lightning struck trees. In observing a core from the north side of a stag headed tree with no external evidence of a trunk scar, the growth ring of 1853 was found to be noticeably

narrower. Narrow rings followed for 15 years and then there was a gradual increase until the presumably normal rate of growth was reattained. On the south side annual rings could be noted after and including 1856. Inward from this for a distance of about two millimeters was a mass of resin, secreted by the tree into the lightning burn. By comparing these findings with those on the north side of the tree, it is evident that the narrow ring of 1853 was the year in which the lightning struck, and the three years difference on the south side was needed for the healing over of the wound at the place where the core was taken. The resin secretion was next to summer wood thus indicating that the lightning must have struck before growth started in the spring of 1853.

In the second type of injury, an unhealed lightning scar was noted on the south side of the trunk. The core from the north side of the tree had a very narrow ring (0.4 mm.) for the year of 1906, which was followed by larger rings (1 mm. each) for a period of four years, then normal growth was resumed up to the time the core was taken. The core from the other side of the tree had a resinous area for 1906, and a scarcely discernible ring for that year. The next season's growth showed a slight influx, then there followed six years of slow growth. From 1913 to the time the core was taken the growth was apparently normal. Thus, one can detect the time of the burn, see the immediate increase of growth in the region which enables the burn to be covered, and observe a slowing down of wood formation in the unburned region of the trunk until the burn is healed. Lightning, then, not only kills a part of the tree, causing an open wound and burn, but also slows down its normal rate of growth and causes a blemish which will be a detriment should the tree be used in the future for lumber.

TYPES OF TREES

Foresters and lumbermen divide *Pinus ponderosa* into the young, more rapidly growing trees which they term "Blackjack" and the more mature, slowly growing trees which they call the "Yellow pine." The age at which a blackjack becomes a yellow pine varies from 100 to 150 years and this in turn is modified by the environmental conditions under which the tree is growing. The blackjack type is distinguished by its darker-colored, and more deeply furrowed bark. The tree has a thicker, lower-branching crown which is often longer and more pointed than the mature type of ponderosa pine. The cork cambiums of the blackjack are narrower and longer and the bark thicker and more solid than in the mature type. This solidity is due to the thinner and more compact "borke" in the blackjack bark. The borke regions of the mature tree, being thicker and spongier, cause its outer bark to be lighter and consequently to scale off more easily than that of the blackjack.

The ponderosa pine is often termed a "rock grower." The seedlings are able to get root hold in the cracks of solid granite and secure enough moisture for continued growth. The top adjusts itself to the root spread, balance is maintained, and the tree lives.

Many rock growers of this general nature are noted whose developing roots are curtailed by the solid rock and consequently are able to secure a very limited amount of water. The top, in order to maintain a balance, has a very restricted foliage, the branches are short and contorted and many of them are dead or in a dying condition. Many of the trees in their struggle for existence have only one cluster of leaves to indicate that life is present. There are hundreds of these rock growers which are of no economic importance to the forester or lumberman but are extremely interesting to both the botanist and general observer as they live for hundreds of years with no obvious sources of materials for existence other than from the solid granite.

EXTREMES

As stated in the beginning of this paper, the ponderosa pine presents many extremes. These are partly discussed under moisture relations in that most rapid growth is found in the fertile valleys and the most retarded growth on the dry, open slopes. The elevation extremes have also been mentioned; the highest of the region was found in the south saddle of Deer mountain at an elevation of 9750 feet. The lowest elevation at which trees were observed was in the lower entrance to the Big Thompson canyon at approximately 5200 feet.

Frequently references are found stating that the ponderosa pine attains a height of over 100 feet with extremes reached in the Sierra Nevada mountains of California where heights of over 200 feet are recorded. In the area studied the tallest trees were all less than 100 feet. Of the 236 trees measured, the tallest one, growing in the Big Thompson canyon, was 92 feet high. The average height of all trees over 100 years old was 40 feet. Rock growers and young trees were not considered in the above average. These data, together with extremes and averages for age, height, and diameter are presented in table 3. Many cores were taken that had over 200 growth rings but few with over 300. Comparing these with the actual diameters and forming an estimate, it does not seem probable that many trees of the area are much over 400 years old. The greatest diameter measured was 50.9 inches and was of a tree growing in the moist valley of Fish Creek. Several other trees of this region approach this diameter and their heights range from 70 to 80 feet. Taller trees were found along the Big Thompson but their diameters were in the range of 30 inches. Other

regions of the locality probably present extremes that would equal or exceed these but to no marked degree.

TABLE 3

Averages and extremes of height, age, and diameter. Measurements breast high

		TREES UNDER 100 YRS. OLD	TREES OVER 100 YRS. OLD	ALL TREES MEASURED
Height	Maximum	60 feet	92 feet	92 feet
	Average	24.08 feet	40.34 feet	36.21 feet
	Minimum	4 feet	2 feet	2 feet
Age	Maximum	98 years	387-years	387-years
	Average	64.9 years	—	—
	Minimum	9 years	100 years	9 years
Diameter	Maximum	18 inches	50.9 inches	50.9 inches
	Average	8.7 inches	18.77 inches	13.75 inches
	Minimum	2.1 inches	4.8 inches	2.1 inches
Number of trees included		98–	138–	236

SUMMARY

A. The growth rate of the ponderosa pine is effected by many factors and the most outstanding of these for the region have been discussed. A brief summary of these is here presented.

1. The elevation at which the ponderosa pine grows ranges from 6000 feet to 8500 feet. This range is governed by moisture and temperature, especially the temperature of the soil at the time of germination and seedling establishment.

2. Slope. The ponderosa pine is found in purest, open, and uneven-aged stands on the south slopes. Mixed stands to isolated specimens are found on the west, east, and north slopes. Pure and mixed stands of limited extent are found along streams and rivers and in the valley sites. Factors governing this distribution are light, temperature, and moisture.

3. The density of the stand is in direct relation to the water supply. Light and temperature are also factors and important in the order named.

4. Growth is proportional to the water supply. This is exemplified by the comparison of equal-aged trees growing in contrasting habitats.

5. The water supply is correlated very closely with composition and quantity of soil. The valleys and lower slopes, coves and regions built up by the accumulation of humus and water-washed soil, contains much moisture, and thus afford the most ideal growing places. Trees growing in dry, barren situations are retarded according to the degree of root and

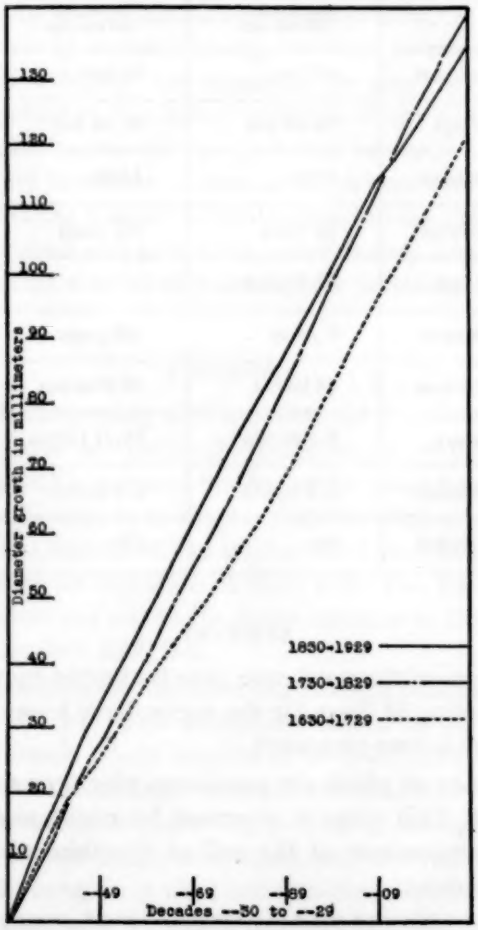

Fig. 4. A comparison of growth per decade for three centuries, 1630 to 1929.

moisture limitations. The extreme of retarded growth is reached in the rocky areas.

B. Factors more directly noted with the individual trees than with the whole area.

1. The form of the tree is modified by the density of the stand, the degree of slope on which the tree is growing, and available light. Eccentric

crown with the balance to the south or downslope side, and the eccentric growth rings with the narrow side to the south or downhill side are the two more obvious results of slope and light conditions.

2. The two chief biotic factors are the bark beetle and the mistletoe. The bark beetle attacks mature trees and either kills them or causes a marked decrease in the rate of growth until the effects of the attack are overcome. The mistletoe causes deformity of branches and bole, general slowing down in the rate of growth, and eventually the death of the tree.

3. Lightning causes "stag head" and tissue destruction by mechanical injury. A period of slow growth follows which is never entirely overcome, especially if the photosynthetic area is altered.

4. The rate of growth is the most marked during the first century of the tree's life. The rate decreases with continued growth and when the rate is materially decreased for a given tree, the summer wood becomes less distinct as compared to the spring wood.

After weighing the various factors that have direct influence upon the normal growth rate of the individual trees, of a stand, and finally of the entire area, one can readily see that any actual growth rate figures given will be very general but representative. The diameter increments of all trees measured are compared for the last three centuries in table 4.

TABLE 4

Millimeters of wood formed per decade for the last 300 years.

DECADE	1920-29	1910-19	1900-09	1890-99	1880-89	1870-79	1860-69	1850-59	1840-49	1830-39	AVERAGE
Century 1929 1830	10.37	10.92	12.82	13.03	11.76	14.08	13.87	13.45	15.74	18.60	14.96
1829 1730	13.60	14.14	14.52	15.61	14.44	13.12	13.83	12.82	13.46	14.56	15.56
1729 1630	13.56	12.21	13.88	13.04	11.47	10.10	9.25	11.53	11.27	15.00	13.57
										Average	14.69

The century growth of the ponderosa pine is shown graphically in figure 4. We observe a very close correlation in the amount of wood formed during the years compared when all trees are considered. If the century 1630 to 1729 could have been represented in more trees, this correlation would undoubtably have been closer than indicated in figure 4. There is not much variation from one decade to the next and the extremes

shown are 9.25 mm. for 1660 to 1669 and a maximum of 18.6 mm. for 1830 to 1839. These figures may have been modified by the decade group being represented in the majority by trees of a moist or dry area. The average diameter growth per decade for the last 300 years, all trees considered, is 14.69 millimeters. The average yearly diameter increment in the ponderosa pine is 1.47 millimeters.

The writer wishes to express his sincere thanks to Dr. Raymond J. Pool, chairman of the Department of Botany, the University of Nebraska, upon whose suggestion this problem was undertaken, and whose counsel was invaluable throughout its progress.[1]

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[1] Contribution from the Department of Botany, University of Nebraska.

The genus Macairea DC. in northern South America

H. A. Gleason

The genus *Macairea*, with twenty-eight described species, is one of the best defined and least known genera in the family Melastomataceae. The reason for the latter condition is simple: the majority of the species are found only in inland South America, especially in the savannas and mountains north of the Amazon, a vast region still inadequately explored. Of the seventeen species listed by Cogniaux forty years ago, eight were known to him through a single collection alone and three others from two collections. More material has become available since then, but more than half of the species are still represented in herbaria only by the type number. *Macairea adenostemon* DC. is well distributed in central and southern Brazil and has often been collected. There are actually more specimens of this one species in the herbaria at Kew and at Berlin than of all the other species together.

The botanical history of the genus begins with the publication of *Rhexia Radula* by Bonpland in 1820. He collected two other species also while in South America with Humboldt, but gave them no names. In 1828 De Candolle erected the genus *Macairea*, defined it exactly as understood at present, and included in it Bonpland's species and three others. The selection of a type from these four offers some little difficulty, since all of them agree well with the technical portion of the generic description. *M. Radula* has the advantage of being the only species previously named and illustrated. This and *M. adenostemon* have leaves strigose or hirsute on the upper side, while the generic description calls for glabrous leaves, such as occur in *M. rufescens* and *M. thyrsiflora*. De Candolle must have had the latter species in mind when he stated that the leaves are subvelutinous beneath, and *M. thyrsiflora* has accordingly been selected as the type. Fortunately the choice of a type is at present of no nomenclatorial significance.

Schomburgk explored British Guiana, southern Venezuela, and northern Brazil in the late thirties and collected five new species. Four of these were described by Bentham in 1840 as *M. multinervia*, *M. pachyphylla*, *M. parvifolia*, and *M. rigida*, and the fifth by Naudin in 1850 as *M. calvescens*. Spruce botanized in the upper Amazon valley in the fifties, collecting six species of *Macairea*. Two of these were already known; *M. Spruceana*, *M. sulcata*, and *M. stylosa* were described by Triana in 1871 and the sixth became the type of *M. albiflora* Cogn. in 1885. Cogniaux reviewed the genus for the Flora Brasiliensis in 1885, describing as new *M. sericea*,

M. ledifolia, and *M. Mosenii* from central and southern Brazil, and *M. albiflora* and *M. foveolata* from the upper Amazon region. This brought the total to seventeen species and no additions had been made by 1891, when his Monograph was published.

Since then eleven species have been described, based in every case on recent collections: *M. Theresiae* Cogn., 1895; *M. aspera* N. E. Br., 1901; *M. glabrescens* Pilger, 1905; *M. scabra* Cogn., 1906; *M. arirambae* Huber, 1914; *M. goyazensis* Hoehne and *M. villosa* Hoehne, 1922; *M. viscosa* Ducke, 1922; *M. duidae* Gl., *M. lanata* Gl. and *M. linearis* Gl., 1931. In almost every case these were discovered in regions previously unvisited or inadequately collected by botanists.

The treatment below does not consider six species known only from central or southern Brazil and adjacent Bolivia, *M. adenostemon* DC., *M. goyazensis* Hoehne, *M. ledifolia* Cogn., *M. Mosenii* Cogn., *M. sericea* Cogn., and *M. villosa* Hoehne. The work is based on the material in the herbaria at New York, Kew, Geneva, and Berlin, and the type or authentic material of every species but one has been examined.

Synonymy scarcely exists in the genus. One species was placed by Naudin in his heterogeneous group *Tetrameris;* De Candolle mentioned a manuscript name, which does not constitute official publication, and Bonpland described the first species known under a different genus. The remaining twenty-five species are entirely without synonyms, a condition seldom found in genera of such size.

Cogniaux' arrangement of the species is based entirely on such characters as pubescence, leaf-venation, length of the calyx, and similar features. He apparently overlooked a point in the structure of the stamens which seems to be of importance and by which two groups may be distinguished with precision. This character has been used below as the basis of the two sections of the genus.

MACAIREA DC. Prodr. 3: 109. 1828

Tetrameris Naud. in part, Ann. Sci. Nat. Bot. III. 14: 120. 1850.

Flowers 4-merous; hypanthium campanulate; calyx and sepals ascending or spreading; petals obovate, triangular-obovate, or broadly elliptic, nearly or quite symmetrical; stamens more or less dimorphic; filaments very slender, arcuate at the summit, one or both series usually glandular-pubescent on the inner side only; anthers very slender, straight or slightly arcuate, opening by a ventro-terminal pore in the short upturned beak; connective greatly prolonged below the thecae and dilated at base into a cordate, ovate, oblong, or hoof-shaped organ which is chiefly posterior, the anterior lobes minute or nearly wanting; ovary free, 4-celled (rarely 3-celled), pubescent or glandular,

at least above (said to be glabrous in one species); style slender, slightly sigmoid, often glandular below; stigma punctiform; seeds cochleate. Bushy or freely branched shrubs with short internodes; leaves usually thick or firm, comparatively small, linear to elliptic or ovate, occasionally rotund; flowers pink to purple, in small or large terminal panicles.

The connective of the short stamens is invariably stout, much shorter than the thecae, curved into a quarter or half circle, terete or shallowly channeled on the ventral side, and gradually dilated at base into a stout, fleshy, hoof-shaped organ, which is narrowly or broadly cordate in outline from the basal direction.

I. Connective of the long stamens very slender, nearly or quite as long as the thecae, abruptly dilated at base into a flat, cordate, ovate, or oblong organ SECTION I.

II. Connective of the long stamens essentially like that of the short stamens in shape but somewhat longer, always distinctly shorter than the thecae SECTION II.

III. Flowers unknown

Leaves glabrous above — 21. *M. stylosa*

Leaves scabrous above — 22. *M. duidae*

SECTION I

Leaves glabrous above, often slightly rugose or marked with crater-like pits, usually resinous-dotted beneath.

Sepals linear.

Leaves 5-pli-nerved; sepals shorter than the hypanthium — 21. *M. stylosa.*

Leaves 3-nerved; sepals twice as long as the hypanthium. — 1. *M. sulcata.*

Sepals triangular.

Strigose hairs of the hypanthium less than 0.5 mm. long; glandular hairs of the ovary very short — 2. *M. thyrsiflora.*

Villous or strigose hairs of the hypanthium 1–4 mm. long; hairs of the ovary increasing distally to 1–2 mm. long.

Leaves acute, pubescent beneath with hairs, 1–1.5 mm. long; strigose hairs of the stem and hypanthium 4–5 mm. long; ovary glandular-hirsute — 3. *M. rufescens.*

Leaves acute, densely resinous beneath; strigose hairs of the hypanthium 1–2 mm. long; ovary resinous and pubescent with simple hairs.

Sepals 1 mm. long; leaves 5-nerved; ovary resinous and villous in the distal half — 4. *M. glabrescens.*

Sepals 2.5 mm. long; leaves 3-nerved; ovary densely strigose throughout, concealing the resin-dots — 5. *M. Spruceana.*

Leaves hirsute or strigose above; pubescence of the ovary not exceeding 0.5 mm. in length, even at the tip.

Hypanthium not resinous-dotted, its longer hairs glandular.

Filaments glabrous; leaves 5–7-nerved.

Leaves acute, 5-nerved; sepals acute; petals 11 mm. long — 6. *M. lanata.*

Leaves rounded above, 7-nerved; sepals obtuse; petals 6 mm. long
7. *M. multinervia.*
Filaments glandular-pubescent; leaves 3-nerved 8. *M. parvifolia.*
Hypanthium copiously resinous, its longer hairs simple.
Sepals linear, much longer than the hypanthium; leaves 5-nerved
9. *M. foveolata.*
Sepals triangular, shorter than the hypanthium; leaves 3-nerved.
Leaves obtuse to rounded or retuse; connective of the larger stamens shallowly 2-lobed posteriorly.
Petals elliptic-oblong; sepals nearly 2 mm. long 10. *M. scabra.*
Petals triangular-obovate; sepals 0.7 mm. long 11. *M. arirambae.*
Leaves acute; connective of the larger stamens not lobed 12. *M. albiflora.*

SECTION II

Leaves glabrous on the upper side.
Leaves smooth above, 20–30 mm. wide 21. *M. stylosa.*
Leaves scabrous above, 2–3 mm. wide; hypanthium and ovary lepidote
13. *M. linearis.*

Leaves hirsute or strigose above.
Hypanthium and stem strigose with closely appressed, simple hairs 14. *M. aspera.*
Hypanthium glandular-pubescent with short spreading hairs; hairs of the stem spreading or curved-ascending.
Sepals broadly triangular to oblong, 2–4 mm. long; ovary 4-celled.
Filaments glandular-pubescent.
Leaves acute; petals 3.5–5 mm. long 15. *M. pachyphylla.*
Leaves obtuse; petals 7–9 mm. long 16. *M. Radula.*
Filaments glabrous; leaves obtuse, attenuate at base 17. *M. calvescens.*
Sepals narrowly triangular, 8 mm. long; ovary 4-celled 18. *M. viscosa.*
Sepals subulate, 3–4.5 mm. long; ovary 3-celled 19. *M. rigida.*

1. MACAIREA SULCATA Triana, Trans. Linn. Soc. Bot. **28:** 38. 1871. Known only from the type number, *Spruce 4004* (K), Tarapoto, Peru.

2. MACAIREA THYRSIFLORA DC. Prodr. **3:** 109. 1828. Venezuela, Esmeralda: *Tate 341* (NY); San Carlos, on the Rio Negro: *Spruce 2952* (K, B, G), *Holt & Gehriger 301* (NY); *Spruce 2953* (G); Upper Rio Negro River, Brazil: *Weiss & Schmidt* (NY); Rio Padawire, northern Brazil: *Schomburgk "no No. 5"* (K); northern Brazil: *Koch 58* (B).

3. MACAIREA RUFESCENS DC. *l.c.* Known only from the type collection, *Spruce 3134* (K, B, G), San Carlos on the upper Rio Negro.

4. MACAIREA GLABRESCENS Pilger, Verh. Bot. Ver. Brand. **47:** 165. 1905. Known only from the type collection, *Ule 6153* (B, K), from "Campina an der Ponta negra," Rio Negro, Brazil.

5. MACAIREA SPRUCEANA Berg apud Triana, *l.c.* Known only from the type collection, *Spruce 2013* (K, B, G, NY), from the Rio Negro, northern Brazil, between San Gabriel and Barcellos.

6. MACAIREA LANATA Gl. Bull. Torrey Club **58:** 416. 1931. Known only from the type collection, *Tate 588* (NY) and *Tate 752* (NY), both from the summit of Mount Duida, Venezuela.

7. MACAIREA MULTINERVIA Benth. Hook. Jour. Bot. **2:** 291. 1840. *Tetrameris trivalvis* Naud. *op. cit.* 121. 1850. Known only from the original collections of Schomburgk on Mount Roraima, British Guiana: *188.5* (type, K), *706* (K, B, G), and *1073* (K, B).

8. MACAIREA PARVIFOLIA Benth. *op. cit.* 293. 1840. Known only from the original collections of Schomburgk on Mount Roraima, British Guiana: *168.5* (type, K), *699* (K, G), and *1089* (K, B).

9. MACAIREA FOVEOLATA Cogn. Fl. Bras. **14**[4]**:** 596. 1888. Not seen by me: the type and only cited collection is *Schwacke-Glaziou 9806*, from the upper Amazon valley.

10. MACAIREA SCABRA Cogn. Engl. Jb. **42:** 133. 1908. Known only from the type collection, *Weberbauer 4708* (B), from Moyobamba, Peru.

11. MACAIREA ARIRAMBAE Huber, Bull. Soc. Bot. Geneve II. **6:** 193. 1914. Alto Ariramba, north of Pará: *Ducke 8003* (type) and *8087* (cited by Huber). Neither of these have been examined by the author and the characters given in the present key are taken from *Ducke 10871*, from Bella Vista, on the Tapajos River, near Pará.

12. MACAIREA ALBIFLORA Cogn. *op. cit.* **14**[3]**:** 246. 1885. Known only from the type collection, *Spruce 3719* (K), from Maypures, on the Orinoco, and from granite rocks along the Atabapo River, Venezuela.

13. MACAIREA LINEARIS Gl. Bull. Torrey Club **58:** 417. 1931. Known only from the type, *Tate 532* (NY), from the summit of Mount Duida.

14. MACAIREA ASPERA N. E. Br. Trans. Linn. Soc. Bot. II. **6:** 27. 1901. Slopes of Mount Roraima, British Guiana: *Quelch & Mc Connell 31* (type, K) and *24* (K); Kaieteur savanna, British Guiana: *Jenman 876* (K).

15. MACAIREA PACHYPHYLLA Benth. *op. cit.* 292. 1840. Mount Roraima region: *Schomburgk 452* (type, K, B, G), *Quelch & Mc Connell 181* (K). *Jenman 1057* (K), *5411* (B), *Ule 8442* (B); Esmeralda, Venezuela: *Tate 323* (NY), 324 (NY).

16. MACAIREA RADULA (Bonpl.) DC. *l.c.* 1828. *Rhexia Radula* Bonpl. Rhex. 107, pl. 41. 1820. Known only from the type collection by Bonpland (B); the place of collection is not known but is probably along the upper Rio Negro, the Casiquiare, or the upper Orinoco.

17. MACAIREA CALVESCENS Naud. *op. cit.* III. **13:** 35. 1850. Known only from the type collection, *Schomburgk 521/823* (K, B, G), from the Roraima region in British Guiana.

18. MACAIREA VISCOSA Ducke, Arch. Jard. Bot. Rio Janeiro **3:** 223. 1922. Known only from the type collection, *Ducke 2398* (K, B), from Prainha, Pará.

19. MACAIREA RIGIDA Benth. *op. cit.* 292. 1840. Northern Brazil or southern Venezuela, "walls of Mount Mazacca": *Schomburgk 1015* (type, K, B, G); summit of Mount Duida: *Tate 769* (NY).

Species imperfectly known

20. MACAIREA THERESIAE Cogn. Bot. Centr. **66:** 369. 1896. Not seen by me; the plant was collected by Princess Therese of Bavaria along the lower Rio Negro in Brazil. Cogniaux' scanty description does not mention the stamens.

21. MACAIREA STYLOSA Triana, *l.c.* 1871. Along the Casiquiare River; *Spruce 3195* (type, K, B, G); along the Orinoco River near the Atabapo; *Bonpland* (B). The chief stated character of the species is the glabrous ovary, but since the only known specimens are in fruit this feature is of doubtful value. Fortunately it may be placed in a key by foliage characters alone.

22. MACAIREA DUIDAE Gl. Bull. Torrey Club **58:** 416. 1931. Known only from the type collection, *Tate 1024* (NY), from the summit of Mount Duida, Venezuela. The specimen is in fruit only.

INDEX TO AMERICAN BOTANICAL LITERATURE
1931–1933

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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